REMNANT SEASHORE VEGETATION OF NORTHWEST COSTA RICA

JONATHAN D. SAUER

Department of Geography, University of California, Los Angeles 90024

The massive literature on coastal vegetation of the world leaves the Pacific side of Central America almost untouched. Presence of mangroves and a few other strand species has been reported from the Golfo de Panamá (Johnston, 1949) and the Golfo Dulce (Allen, 1956). A single schematic profile of mangrove zonation is available from the coast of El Salvador (Gierloff-Emden, 1974); the rest of the coastal vegetation is blank for 2,000 km between the rainforest region of Golfo Dulce and the thorn-scrub region of western Mexico, where reconnaissance studies again list some coastal species (Turner, 1960; Rzedowski and McVaugh, 1966). The transects to be discussed here sample a small, 30 km long sector of that blank, located on the seasonally dry Guanacaste coast. These transects, done in 1972, were intended to salvage information on what remained of the spontaneous seashore vegetation before it was too late.

With Costa Rican government encouragement, this beautiful and formerly inaccessible coast is being promoted as a prime attraction for local and foreign tourists and retired people. In 1972, the largest beach in the sector was being internationally advertised as "Playa Grande Estates, the American way of life brought to Costa Rica by American developers". The coastal thicket had been bulldozed to stake out sites for 400 homes, a luxury hotel, and a country club. For a long time the region has had a few modest beach resorts, such as Playas del Coco, with dry weather road access but they were far apart and wild stretches lay between. New airstrips and all-weather roads are rapidly opening the wild stretches to development. Presumably the native seashore vegetation will soon give way to the pool of cosmopolitan ornamentals and weedy plants that have been spread around the tropics since Columbus. At Plavas del Coco, for example, the beach houses are surrounded by East Indian almonds (Terminalia catappa), Madagascar flambovants (Delonix regia), South Pacific crotons (Codiaeum variegatum), African Bermuda grass and tamarinds (Cynodon dactylon and Tamarindus indica), and Indo-Pacific coconuts (Cocos nucifera).

Whether coconut palms are members of the natural vegetation of this coast is unclear. When Balboa crossed the isthmus, there were wild coconut groves farther south on the Pacific coast of Costa Rica and Panamá, evidently volunteers from sea-drifted nuts (Patiño, 1963; Sauer, 1971). The prevailing current would have carried nuts from those groves up along the Guanacaste coast, so that the species may have grown here spontaneously also. If so, it is one member of the natural vegetation that is becoming commoner along the sea as a result of human planting. Vegetational transects were run at right angles to the shore in the form of continuous belts, 1 m wide, in eight sectors between Boca Venado $(10^{\circ}9' \text{ N})$ and Bahia de Culebra $(10^{\circ}36' \text{ N})$. Multiple transects, spaced at least 100 m apart, were made in physiographically complex sectors. Type of substrate, species present, estimated cover, and maximum plant height were recorded for each square meter along the transects. Each transect was unique in detail but a few selected transects (figs. 1–5) show most of the range of diversity encountered. Transects were placed without regard to vegetational composition except that areas of obvious severe artificial disturbance were avoided.

It should not be implied that much of the coastal vegetation was in a pristine state at the time of study. The Guanacaste region was the home of ancient high civilizations that gave way during the Spanish colonial period to small cattle ranches and subsistence farms. The seasonal forest has been greatly affected by clearing for pasture and shifting cultivation. However, the ranchers left some fringes of vegetation along tidal estuaries, beaches, and rocky headlands; these will be discussed in that order.

INTERTIDAL WOODLAND

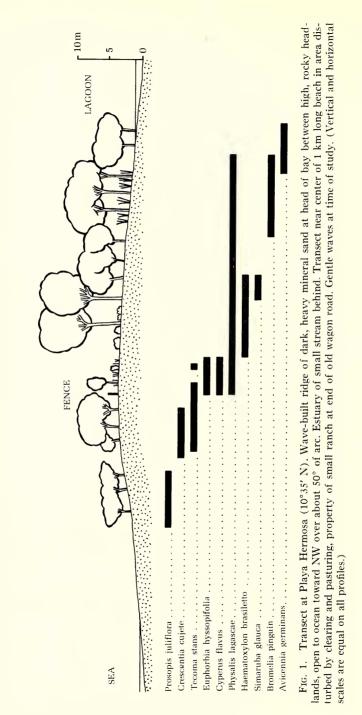
In spite of a mean tidal range of about 2 m, the rugged topography and steep stream gradients confine mangroves to small stands that do not compare in extent with the swamps on the inland side of the Nicoya peninsula. However, the dominant species are the same: *Rhizophora mangle*, *Avicennia germinans*, and *Laguncularia racemosa*. Less expectedly, *Laguncularia* trees were also found rooted in rock crevices that are washed by waves on the shore of the large, open Bahia de Tamarindo. Elsewhere, on fairly open sandy beaches, some other trees and shrubs were also found growing within reach of the waves at high tide: *Hippomane mancinella* on Playa Hermosa and Playa Panamá, *Hibiscus tiliaceus* at Boca Venado, and *Conocarpus erectus* on Punta San Francisco. In the Caribbean, these three species are commonly associated with mangroves on inner margins of tidal swamps; they also grow on less sheltered coast there, but only above the high tide mark.

SAND FLAT VEGETATION

Beach progradation by wave upwash has built stabilized sand flats or plateaux at the heads of many coves and bays along this coast. The sand ranges from tan to nearly black, depending on proportions of quartz, shell, and heavy minerals.

On the most sheltered bays, the sand flat vegetation, behind whatever intertidal trees may be present, shows no special coastal character in either physiognomy or floristics. The dominant species are all common members of inland thorn scrub and seasonal woodland communities. Most of them range widely through Central America, Mexico, northern South America, and the West Indies. The mesquite (*Prosopis juliflora*),

1975]



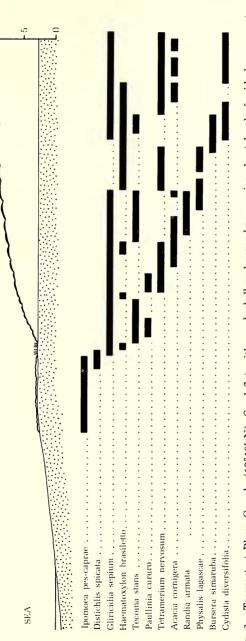


FIG. 2. Transect at Playa Grande (10°19' N). Sand flat with much shell and some heavy minerals at head of wide bay, open to ocean over about 100° of arc. Transect beyond edge of bulldozed area near south end of 3 km long beach. Thicket has similar composition for nearly 500 m farther inland to edge of estuary fringed by Capparis odoratissima trees. On 1955 aerial photograph, this sand flat appears as cleared pasture. Moderate surf at time of study.

10 m

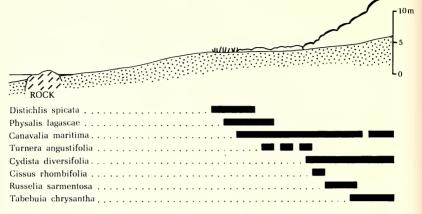


FIG. 3. Transect at Punta Cerritos $(10^{\circ}9' \text{ N})$. Cove beach of dark, heavy mineral sand and shell on low, rocky point, open to ocean toward SW over about 120° of arc. Moderately heavy surf at time of study.

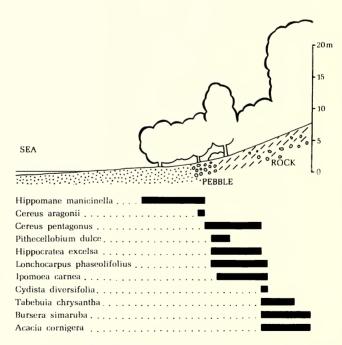


FIG. 4. Transect at Playa Pedregosa (10°34' N). Narrow beach of heavy mineral sand and a little shell material over metamorphic bedrock, open to ocean toward NW over about 50° of arc. Transect half way between head of bay and tip of head-land. Moderate waves at time of study.

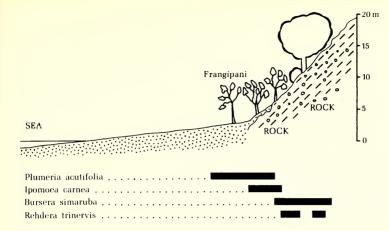


FIG. 5. Transect at Playas del Coco $(10^{\circ}33' \text{ N})$. Coral rubble and shell mixed with dark sand over metamorphic bedrock, open to ocean toward N over about 15° of arc. Transect on S side of Bahia El Coco half way between its head and Punta Centinela. Gentle waves at time of study.

calabash tree (*Crescentia cujete*), and other species on a Playa Hermosa transect (fig. 1) are examples, as are *Pithecellobium dulce* and *Bursera simaruba*, which do not appear on this particular transect but were common dominants on several sheltered sand flats.

On more exposed shorelines, the sand flat vegetation displays rudiments of the classic beach zonation, with outpost vines and creepers backed by a spray-shorn thicket (figs. 2–3). The outpost zone is exceptionally narrow and poor in species. It has the pantropical beach morning-glory and sea-bean (*Ipomoea pes-caprae* and *Canavalia maritima*) and the common New World seashore saltgrass (*Distichlis spicata*). The few other species found in this zone are primarily pioneer herbs of open inland sites, the most abundant being *Physalis lagascae*, *Euphorbia dioica*, and *Pectis grandiflora*. In the thicket behind the outpost zone, the only abundant peculiarly coastal species is the pantropical gray nicker-bean (*Caesalpinia bonducella*). These thickets, like those on more sheltered bays, are dominated by species that range widely through tropical America in inland scrub formations, especially on limestone.

ROCKY PROMONTORIES

Headlands between the bays have outcrops of metamorphic rock and talus slopes. These are the habitat of two primarily coastal cacti, the wide-ranging *Cereus pentagonus* and the endemic *C. aragonii*. On the most exposed headlands, these cacti are joined by two succulent monocots (*Fourcroya cabuya* and *Bromelia pinguin*) that are shared with rocky inland sites. On less exposed slopes, the cacti are joined by frangipani (*Plumeria acutifolia*) and other species shared with sand flats and inland scrub (figs. 4-5).

DISCUSSION AND CONCLUSIONS

This region's impoverished seashore flora can hardly be blamed on geographic isolation and lack of insemination. Several strictly coastal Atlantic-Caribbean species are represented, namely the three mangroves and two associates, *Hippomane mancinella* and *Conocarpus erectus*. These were evidently dispersed by ocean currents before interposition of the present isthmus; other members of the rich Caribbean seashore flora could presumably have immigrated the same way had the region been hospitable to them. We know in fact that lack of dispersal is not responsible for absence of the most important of all Caribbean seashore species, the sea-grape (*Coccoloba uvifera*). This species was deliberately introduced to the Pacific coast and old trees are commonly seen planted around beach houses but the seedlings do not establish themselves in natural habitats here.

Four other species adapted for long-range ocean dispersal are shared not only with the Caribbean but with tropical coasts in general: *Canavalia maritima*, *Caesalpinia bonducella*, *Hibiscus tiliaceus*, and *Ipomoea pes-caprae*. These four, like the coconut, may have arrived from the west across the Pacific. They are all present on Cocos Island off Panamá (Fosberg and Klawe, 1966), where the Equatorial Counter Current coming from the west turns northward to sweep along this coast.

I believe the rudimentary character of the distinctively coastal vegetation of this coast is due simply to lack of storms and of onshore winds. Tropical cyclones occasionally develop in this general region but they usually form well offshore and move far away to the west before generating gale or hurricane force winds (U.S. Navy Hydrographic Office, 1964). Heavy surf must be rare as the upper limit of old, stranded drift is barely above normal high tide mark. The mangroves and associates noted as standing within wave reach on only partly sheltered beaches also bear witness to absence of high energy waves. In other words, the storm beach zone, the normal habitat of much of the world's coastal pioneer flora, is virtually missing here.

The coast also provides peculiarly little opportunity for the salt spray community. During the dry season, when salt spray should be most effective in driving back ordinary inland pioneer species, winds are prevailingly from the northeast, i.e., offshore. During the rainy season, from May to October, wind directions are more variable but velocities are normally weak. Some spray shear is evident on thicket canopies on exposed headlands and behind the more open beaches but a very little spray might produce this effect on the thin-leaved species present. In short, a rugged, storm-free, lee coast offers a vanishingly narrow habitat for specialized seashore plants.

However, it does not follow that this coast has played an insignificant role in evolution and migration of pioneer plants. The edge of the land offers pioneer species an opening that is relatively permanent and spa-

KEIL: PECTIS

tially continuous compared to many of the habitats they colonize in inland succession. Even if relatively small, coastal subpopulations may have been crucial links in spread and survival of their species.

Acknowledgments

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REVISION OF PECTIS SECT. HETEROPECTIS (COMPOSITAE: TAGETEAE)

DAVID J. KEIL

Biology Department, Franklin College, Franklin, Indiana 46131

Pectis L. sect. *Heteropectis* A. Gray is one of the smallest and most geographically restricted sections of *Pectis*. Comprising only two species, sect. *Heteropectis* is centered in the Sonoran Desert and only slightly exceeds the boundaries of that zone. No other section of the genus is known to occupy such a limited geographical range.